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Factors Responsible for Phosphorus Uptake Efficiencies of Crop Species in Hot Sub Humid Eco-region of Middle Gangetic Plains of India

Avinash Kumar Rai, Amitava Rakshit*, Sumit Rai, Manoj Parihar and Visal Seth

Department of Soil Science and Agricultural Chemistry,
Institute of Agricultural Science, Banaras Hindu University, Varanasi - 221005, India.

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Phosphorus often limits the achievement of high crop yields in low P supplying soils, where P is strongly fixed and largely unavailable for crop uptake. These soils may not be low in total P, but most of it is present in a form of extremely low solubility of Fe/Al or Ca phosphate. This may result in low P uptake. Even varieties of same species differ in their P efficiency i.e. ability to grow well at low P supply. These differences in P efficiency may be based on differences in the internal P requirement, the uptake efficiency and/or the rate of shoot growth. Several researchers have reported that differences in P efficiency are based on size and type of the root system i.e. root length, root radius and root hair density and rate of shoot growth rate . This shows that a number of reasons may contribute to differences in P efficiency among plants, and that those differences may arise at different stages of the growing cycle. Therefore, the aim of this study was to determine the phosphorus efficiency of wheat, maize and pea ,the factors and mechanisms responsible for the observed differences in P efficiency by measuring shoot and root properties during the growing cycle. To achieve these objectives, pot experiments were conducted with wheat ,maize and pea during November 2011 to May 2013 in an acid soil of eastern Uttar Pradesh at the Department of Soil Science & Agricultural Chemistry, Institute of Agricultural Sciences, BHU, Varanasi, India. Main problem of this soil is a low fertilizer use efficiency due to P fixation mainly by oxide and hydro-oxide of iron and aluminum ,which are abundant in this soil .The soil has 14 - 16 %clay, organic carbon, 0.35 % and pH (H_2O)5.3. Treatments consisted of three P levels, P-0 (unfertilized, without P), P-50 (50 mg P/kg soil) and P-200 (200 mg P/kg soil) as potassium di hydrogen phosphate, four harvest intervals (covering the whole crop growth period) and 4 replications for wheat, maize and pea. Comparing the P uptake of different species at limiting P supply, i.e. mainly on the unfertilized plot, maize was able to absorb significantly higher amount compared to wheat or pea. From the model calculation it is pertinent that at P-0, in most cases the measured influx was higher, in maize up to nine times, than the calculated influx. For pea it was almost five times and in wheat it was close to three times. Reasonably good agreement between calculated and measured P influx into the roots of all crops was obtained at medium as well as high P levels.

Keywords: Phosphorus use efficiency, Mycorrhiza, Phosphorus influx and P uptake.

In our experiment with acid soils of Chandauli district of Uttar Pradesh, India (Rai,2015) we have reported that plant species differed in their P uptake efficiencies. Among the plant species studied Maize had the highest P uptake at limiting P supply. At the beginning of the growing season maize was very P inefficient but turned very P efficient later. Comparing the P uptake of different species at limiting P supply, i.e. mainly on the unfertilized plot, maize was able to absorb

* To whom all correspondence should be addressed.
E-mail: amitavar@bhu.ac.in

significantly higher amount compared to wheat or pea. The differences in P uptake efficiency could be due to plant properties involved in P uptake. The P uptake by plants is the result of interactions between plant and soil. The root morphological parameters like root length, root radius, root growth rate, half distance between the root play an important role in P uptake. Besides morphological parameters, physiological parameters which includes maximum influx (I_{max}), Michaclis Menten constant (K_m), and minimum soil solution concentration (C_{min}) has great influence on P uptake. The main soil parameters that influenced in P uptake are soil solution P (Cli), diffusion coefficient (Dc) and buffer power (b) of the soil. The effect of these parameters can be investigated through mathematical models (Claassen and Barber, 1976; Cushman, 1979). These models are based on mass flow and diffusion process and follow the Michaeles Menten kinetics. In these models roots are assumed to be smooth cylinders absorbing nutrients at the rates determined by the nutrient concentration in soil solution. Schenk and Barber (1979) used Claassen- Barber model for predicting P uptake and found a satisfactory prediction. However, under low P conditions model under predicted the uptake. Under prediction could be due to the non inclusion of root hair in the model calculating the P uptake. Claassen (1990) developed a model which also includes the P uptake by root hairs. Fohse et al. (1991) used this model for predicting the P uptake for different species. They reported that predicted influx was close to the observed influx when root hairs were included in the model. The effect was more pronounced in species like spinach with more number of root hairs than species like onion and bean with less number of root hairs. Singh and Sadana (2000) also found better prediction of P uptake by wheat when root hairs were included in model calculations.

Besides root morphological and physiological parameters other factors responsible for variation in P uptake by plant might be mycorrhizal infection of roots and excretion of some organic acids by roots which increases the solubility of P in the soil. Jakobson (1986) found that dry matter production and P uptake by pea was significantly improved by mycorrhizal infection under low P level, however the finding of Guillenmin et al (1995) shows that inspite of having high mycorrhizal infection, the growth of plant was not affected in soybean and pineapple.The objectives of the present study were to investigate the effect of different soil and plant parameters for P uptake by different crop species by using the Claassen model (1990).

MATERIALS AND METHODS

Pot experiments were carried out in the net house using a factorial complete randomized design with crop species and P fertilizer level. Treatments consisted of three P levels, P-0 (unfertilized, without P), P-50(50 mg P/kg soil) and P-200 (200 mg P/kg soil) as potassium hydrogen phosphate, four harvest intervals (covering the whole crop growth period) and 4 replications for wheat, maize and pea. Nitrogen was applied at the rate of 100 kg ha^{-1} for wheat and maize, and 20 kg ha^{-1} for pea and potassium at the rate of 50 kg ha^{-1} for all crops. Besides that calcium and magnesium were applied at the rate of 1 mg kg^{-1} soil. Micronutrients including Zn, Fe, Cu, B, Mn and Mo were applied at the rate of 0.5 mg kg^{-1} soil. After application of fertilizers to pots, seeds of varieties HUW-468 for wheat, NMH-51 for maize and HUDP-15 for pea were sown in pots. To run the model (NST 3.0) soil and plant parameters are needed.

The model is based on the transport equation of Nye and Marriot (1969) extended by a term A to take uptake by root hairs into account (Claassen and Steingrobe, 1999):

$$b\Delta C_l/\Delta t = 1/r * /\Delta r * (r * D_e *b (\Delta C_l)/\Delta r + r_o * V_o * C_l)-A$$

where,

C_l is the soil solution concentration,

b is the Buffer power,

ris the radial distance to the root axis,

D_e is the effective diffusion coefficient,

V_o is the water flux across the root surface and

r_0 is the root radius.

The sink term A for root hair uptake uses a steady-state approach that allows the use of Michealis-Menten kinetics also for uptake by root hairs (Claassen and Steingrobe, 1999).

Following section shows, how they were obtained.

Soil parameters

Diffusion coefficient in water (Dl, cm^2 s^{-1})

was taken from (Barber 19 80).

Soil volumetric water content (O, cm^{-3}) was determined in the field using granimetric method.

Impedance factor (f) was calculated after Barraclough and Tinker (1981) from the relationship of f = 1.580-0.17 which holds good for sandy loam soil

Soil solution P concentration (Cli) : Soil solution was collected using the Adams ( ) displacement method and was analyzed using spectrophotometers for P concentration.

Buffer power : It was calculated using the following equation $b= P_s/Cli$

Where P_s is the solid P and Cli is the soil solution P.

Plant Parameters

Rate of eater uptake (V_o, cm^3, cm^{-2}, s^{-1}) was taken from (Jungk,1974).Since mass flow is very low for P uptake, an accurate determination of V_o seems not necessary.

Maximum influx (I_{max}, mol $cm^{-2}s^{-1}$) was derived from maximum influx measured on the P_{400} plots and increased by 5% for infinite value. For low P level influx of P_{400} plots was multiplied by two since I_{max} of P deficient plants is higher than that of P sufficient plants (Jungk, 1974). The root surface area, including that of root hairs, in order to express Imax per cm2 divided the influx measured in the field mol cm-1s-1.

Michaclies-Menten constant ($K_{m,\ mol\ cm}{}^{-3}$) . For maize value was taken from Jungk (1974). For other species the same value was used since Jungk (1974) showed that only small differences existed among several species.

Minimum soil solution concentration (C_{min}, mol/cm^{-3}) was also taken from Jungk (1974).

Root radius (r_o) cm: It was measured using a microscope. Average half distance among the neighboring roots (r_1 cm) was calculated using the following formula : $r_1 = 1/$ Ö (RL_v), where RL_v is the root density.

The actual r_1- value was much higher as the extension of the depletion zone so that to facilitate the calculation are r_1 of 0.25 cm was taken for wheat and maize and 0.35 cm for groundnut.

Initial root length (L_o) is the root length in one square meter at the first harvest.

Root growth rate (k,),(cm $m^{-2}d^{-1}$) was calculated from increase in root length between any two harvests . Following formula was used.

$GR_r = (RL_2-RL_1)/(t_2-t_1)$

Where

GR_r = root growth rate (cm m^{-2} d^{-1}), RL is the root length, t = time (days).

Subscripts 1 and 2 refer to current and previous harvests.

Root Hairs

Undistributed soil samples with roots were initially suspended in water for 24 hours and after wards a large number of roots with root hairs were carefully taken by hand. A portion of the fresh root was cut into 1-cm pieces for each treatment and all replications. Each piece of root was laid on one side of a micrometer grid and the intersections of root hairs with the parallel and perpendicular grid lines were counted under a microscope. From the number of intersections the root hair density at different distances to the root surface can be calculated.

RESULTS AND DISCUSSION

In our experiment , we found that maize was more efficient in utilizing P from P-0(control) plots compared to wheat and groundnut. Maize had the highest P uptake at limiting P supply. At the beginning of the growing season maize was very P inefficient but turned very P efficient later. Comparing the P uptake of different species at limiting P supply, i.e. mainly on the unfertilized plot, maize was able to absorb significantly higher amount compared to wheat or pea. In this paper we will discuss the possible the reasons which led to greater P uptake efficiency of maize.

Size of the root system

The supply of mineral nutrients to plants is the result of interactions between two complex phenomena: availability of the nutrients in soil and the ability of plants to absorb the nutrients. Both soil and plant properties are therefore, important for the nutrition of plants. Jungk and Claassen (1997) showed that the main plant properties affecting uptake of nutrients from soil were kinetics of ion absorption by roots, the size of root system and morphological root properties.

To quantify the root system the root length was measured (Table 1) at different growth stages. Root length of all the three species increased with P fertilization. For all species, root length increased with the advancement of crop age up to the middle of the season. Maximum root length was observed at third harvest for all three species thereafter it decreased which was also confirmed by root growth study . For maize it reached up to 3451 m plant^{-1}, followed by wheat (3012 m plant^{-1}) and pea (1872.8 m plant^{-1}) during the third harvest. Irrespective of the P level the size of the root system of pea was only one third that of maize and more one fourth that of wheat. Under no fertilized P (P-0) the root system of pea was only 25-33% of that of maize but the P uptake was almost same for both pea and maize up to third harvest. Even through wheat had the lower size of root system as that of maize, but P uptake was more than for wheat than maize in the second and third harvest. P uptake was highest in the final harvest for maize followed by wheat and pea. This shows that the observed differences in total P uptake cannot be explained by the size of the root system. The absolute size of the root system not always is suited to characterize the roots concerning their function as supplier of nutrients to the shoot because the size of plants or their growth rate may be very different. At a given time roots only have to provide nutrients to the new produced shoot. Treseder (2013) outlined the response ratio of root biomass and soil P content rose exponentially as root length increased. The higher root length (Chapin, 1980; Ehleringer and Monson, 1993; Aerts, 1996) could elicit higher total P content within the plant by increasing the internal requirement. Soil P supply had a great influence on root length.

Table 1. Root length (cm/plant) of wheat, maize and pea at no P (P-0), 50 mg P kg^{-1} (P-50) and 200 mg P kg^{-1} (P-200) application to the soil

I Harvest P levels (mg kg^{-1})	Crops Wheat	 Maize	 Pea
P_0	766.7	452.8	148.5
P_{50}	1189.3	628.3	516.0
P_{200}	1877.9	822.1	852.8
Average	1277.9	634.4	505.8
	C	P	C×P
SEm±	29.3	29.3	50.8
LSD (0.05)	87.1	87.1	150.9
II Harvest			
P_0	867.4	1026.5	266.5
P_{50}	1319.9	1313.9	579.2
P_{200}	2820.3	1756.9	1020.3
Average	1669.2	1365.8	622.0
	C	P	C×P
SEm±	30.3	30.3	52.5
LSD (0.05)	90.1	90.1	156.1
III Harvest			
P_0	889.4	1174.4	829.8
P_{50}	1543.7	1730.5	1483.8
P_{200}	3012.4	3451.2	1872.8
Average	1815.2	2119.7	1395.5
	C	P	C×P
SEm±	40.5	40.5	70.1
LSD (0.05)	120.2	120.2	208.3
IV Harvest			
P_0	749.3	850.5	655.2
P_{50}	1479.0	1247.1	979.0
P_{200}	2069.1	2030.8	1777.0
Average	1432.5	1376.2	1137.1
	C	P	C×P
SEm±	43.7	43.7	75.7
LSD (0.05)	129.8	129.8	NS

Table 2. P influx(10^{-13}mol cm^{-1} s^{-1}) of wheat, maize and pea at no P (P-0), 50 mg P kg^{-1} (P-50) and 200 mg P kg^{-1} (P-200) application to the soil

I –II Harvest P levels (mg kg^{-1})	Crops Wheat	 Maize	 Pea
P_0	1.75	0.93	2.52
P_{50}	2.19	1.94	2.71
P_{200}	2.09	4.63	2.73
Average	2.01	2.50	2.66
	C	P	C×P
SEm±	0.17	0.17	0.29
LSD (0.05)	0.50	0.50	0.87
II –III Harvest			
P_0	1.80	1.21	1.60
P_{50}	1.82	1.25	1.02
P_{200}	2.02	2.27	1.54
Average	1.95	1.43	1.42
	C	P	C×P
SEm±	0.16	0.16	0.27
LSD (0.05)	0.46	0.46	NS
P levels (mg kg^{-1})	Crops		
P_0	0.67	1.10	0.55
P_{50}	0.29	0.30	0.58
P_{200}	0.35	0.40	0.66
Average	0.34	0.60	0.596
	C	P	C×P
SEm±	0.10	0.10	0.18
LSD (0.05)	0.30	0.30	0.52

Phosphorus influx

The efficiency with which each root segment absorbs P is given by the P uptake per unit length and per unit time, the influx (In). The P influx is shown in Table 2. At high P in soil (P-200) the supply to the root is no limiting factor and the P influx is a measure of the demand the shoot puts on the root even though some luxury consumption may occur. At low P in soil (P-0), though, the soil is limiting the supply to the root and the influx then shows to which extent a root is able to extract P from the soil at low P availability.

In the early stage P influx at high P (P-200) was highest for maize, i.e. its demand on root was highest, but at low P the influx was very small. In this stage maize roots could not absorb much P from soil of low P availability and probably was the reason for its little growth in that stage. In the middle of the season the P influx at P-0 increased 6 times and almost reached the maximum value, i.e.

Table 3. Plant and soil parameters used for nutrient uptake model calculations at different soil P levels in Wheat

Parameters	P-0			P-50			P-200		
	I-II	II-III	III-IV	I-II	II-III	III-IV	I-II	II-III	III-IV
Plant									
I_{max} (10^{-6} µmol cm^{-2} s^{-1})	4.38	4.46	0.88	4.38	4.46	0.88	4.38	4.46	0.88
K_m (10^{-3} µmol cm^{-3})	2.40	2.40	2.40	2.40	2.40	2.40	2.40	2.40	2.40
C_{min} (10^{-4} µmol cm^{-3})	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00
r_0 (cm)	0.0146	0.0126	0.0110	0.0161	0.0128	0.0111	0.0168	0.0130	0.0111
r_1 (cm)	0.30	0.27	0.25	0.30	0.27	0.25	0.30	0.27	0.25
RL_0 (cm)	766.7	867.4	889.4	1189.3	1319.9	1543.7	1877.9	2820.3	3012.4
k (cm m^2 d^{-1})	3.36	0.88	-3.11	4.35	8.95	-1.44	31.41	7.68	-20.96
v_0 (10^{-7} cm^2 cm^{-2} s^{-1})	7.5	7.5	7.5	7.5	7.5	7.5	7.5	7.5	7.5
Soil									
C_{Li} (10^{-3} µmol cm^{-3})	1.4	1.4	1.4	4.2	4.2	4.2	116	116	116
D_L (10^{-6} cm^2 s^{-1})	8.9	8.9	8.9	8.9	8.9	8.9	8.9	8.9	8.9
θ cm^3 cm^{-3}	0.21	0.22	0.22	0.21	0.22	0.22	0.22	0.22	0.22
f	0.16	0.16	0.16	0.16	0.16	0.16	0.16	0.16	0.16
b	450	515	635	305	365	475	288	315	335

Table 4. Plant and soil parameters used for nutrient uptake model calculations at different soil P levels in maize

Parameters	P-0			P-50			P-200		
	I-II	II-III	III-IV	I-II	II-III	III-IV	I-II	II-III	III-IV
Plant									
I_{max} (10^{-6} µmol cm^{-2} s^{-1})	9.26	3.92	2.58	9.26	3.92	2.58	9.26	3.92	2.58
K_m (10^{-3} µmol cm^{-3})	2.40	2.40	2.40	2.40	2.40	2.40	2.40	2.40	2.40
C_{min} (10^{-4} µmol cm^{-3})	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00
r_0 (cm)	0.0156	0.0121	0.0110	0.0156	0.0121	0.0110	0.0158	0.0126	0.0110
r_1 (cm)	0.30	0.27	0.25	0.30	0.27	0.25	0.30	0.27	0.25
RL_0 (cm)	452.8	1026.5	1177.36	628.3	1313.9	1730.51	822.1	1756.9	3451.2
k (cm m^2 d^{-1})	19.12	6.04	-7.26	22.85	16.66	-10.74	31.16	67.77	-31.56
v_0 (10^{-7} cm^2 cm^{-2} s^{-1})	7.5	7.5	7.5	7.5	7.5	7.5	7.5	7.5	7.5
Soil									
C_{Li} (10^{-3} µmol cm^{-3})	1.4	1.4	1.4	3.8	3.8	3.8	71	71	71
D_L (10^{-6} cm^2 s^{-1})	8.9	8.9	8.9	8.9	8.9	8.9	8.9	8.9	8.9
θ cm^3 cm^{-3}	0.21	0.21	0.22	0.21	0.21	0.22	0.21	0.22	0.22
f	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18
b	452	525	675	265	325	420	275	327	345

that of P-200. Roots therefore were able even at P-0 to supply enough P to the shoot to obtain almost maximum growth . After 81 days the influx decreased and was at P-0 almost twice that at P-200.

In contrast to maize, pea showed in the early stage at P-0 a relatively high influx which was similar to that at P-200. The same happened in the middle of the season. But in late season the P influx at P-0 was almost nil and only one fifth of that at P-200. This high influx at early stages and low influx later seems to be the explanation of the high growth of pea at P-0 in early and middle season and of the strong reduction in the grain filling stage. Wheat showed at P-0 an intermediate P influx in early and middle season. In late season the P influx at P-0 was more than twice that of P-200 but probably not high enough to support maximum growth as of P-200 . The higher growth at the grain filling stage of the P-200 treatment than P-0 in spite of having a lower P influx probably may be due to high P concentration in the plants during early stages which was used for later growth.

From the results shown, the P influx seems to be a major factor that explains different growth patterns along the growing season for the three species studied.

Table 5. Plant and soil parameters used for nutrient uptake model calculations at different soil P levels in pea

Parameters	P-0			P-50			P-200		
	I-II	II-III	III-IV	I-II	II-III	III-IV	I-II	II-III	III-IV
Plant									
I_{max} (10^{-6} µmol cm^{-2} s^{-1})	5.46	3.26	1.32	5.46	3.26	1.32	5.46	3.26	1.32
K_m (10^{-3} µmol cm^{-3})	2.40	2.40	2.40	2.40	2.40	2.40	2.40	2.40	2.40
C_{min} (10^{-4} µmol cm^{-3})	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00
r_0 (cm)	0.0118	0.0111	0.0106	0.0129	0.0121	0.0117	0.0130	0.01214	0.0117
r_1 (cm)	0.35	0.35	0.35	0.35	0.35	0.35	0.35	0.35	0.35
RL_0 (cm)	148.5	266.5	829.8	516	579.2	1483.8	852.8	1020.3	1872.8
k (cm m^2 d^{-1})	5.90	28.17	-5.82	3.16	45.23	-16.83	8.38	42.63	-3.11
v_0 (10^{-7} cm^2 cm^{-2} s^{-1})	7.5	7.5	7.5	7.5	7.5	7.5	7.5	7.5	7.5
Soil									
C_{Li} (10^{-3} µmol cm^{-3})	1.9	1.9	1.9	4.7	4.7	4.7	87	87	87
D_L (10^{-6} cm^2 s^{-1})	8.9	8.9	8.9	8.9	8.9	8.9	8.9	8.9	8.9
θ cm^3 cm^{-3}	0.23	0.24	0.22	0.23	0.24	0.22	0.23	0.24	0.22
f	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18
b	525	565	615	312	305	325	290	335	365

Table 6. Measured and calculated phosphorus influx by three crops at different harvest intervals

Crop	Harvest interval	Influx (10^{-13} mol cm^{-1} s^{-1})					
		Measured			Calculated		
		P-0	P-50	P-200	P-0	P-50	P-200
Wheat	I-II	1.75	2.19	2.09	0.61	1.97	2.10
	II-III	1.80	1.82	2.02	0.50	1.63	2.01
	III-IV	0.67	0.29	0.35	0.21	0.27	0.33
Maize	I-II	0.93	1.94	4.63	0.10	1.49	4.69
	II-III	1.21	1.25	2.27	0.54	1.01	2.26
	III-IV	1.10	0.30	0.40	0.21	0.28	0.37
Pea	I-II	2.52	2.71	2.73	0.54	2.45	2.78
	II-III	1.60	1.02	1.54	0.21	1.14	1.58
	III-IV	0.55	0.58	0.66	0.13	0.55	0.67

Modeling P influx

The model calculates soil transport of P towards the root by mass flow and diffusion taking sorption of P to soil matrix into account. The different soil and plant parameters were used to evaluate nutrient uptake model for simulating P influx in to the roots of maize, wheat and pea(Table3,4 and 5) Uptake of P is described by a modified Michaelis-Menten kinetic. At P-0, in most cases the measured influx was higher, in maize up to nine times, than the calculated influx. For pea it was almost five times and in wheat it was close to three times. Reasonably good agreement between calculated and measured P influx into the roots of pea was obtained at medium as well as high P levels. This indicates that the nutrient uptake model describes P transport in the rhizosphere satisfactorily.

At P-50 the calculated values (Table 6) became much closer to the measured values; only maize up to midseason still had an influx almost 1.2 to 1.3 times higher than calculated. The reason for such under prediction is not model incompetence. This can be deduced from the good agreement between observed and predicted influx in high P soils. The higher measured than calculated influx indicates that plants posses mechanisms that enhance P transport to the root above that allowed for by the bulk soil. Possible reasons for this enhanced transport may be through root exudates that increase P solubility in the rhizosphere or mycorrhiza symbiosis. It can be seen at P-0 that wheat showed this enhancement right from the beginning of the growing season while maize needed a longer period of P stress in order to adapt to the low P supply and develop those mechanisms that enhance P transport to the root. P showed the enhancement of P influx right from the start and still increased it further later. The higher value of measured influx as compared to predicted influx indicates that P uptake has not been solely influenced by the processes as described by the model, i.e., the increased influx. Plant also possesses mechanisms that enhance P transport to the root in addition to that happens in the soil. Possible reason for this enhanced transport may be, association of mycorrhizal fungi or through root exudates that increase P solubility in the rhizosphere as suggested by several authors (Ryan *et al.,* 2001; Uren and Reisenauer, 1988; Gerke *et al.*, 1994).

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